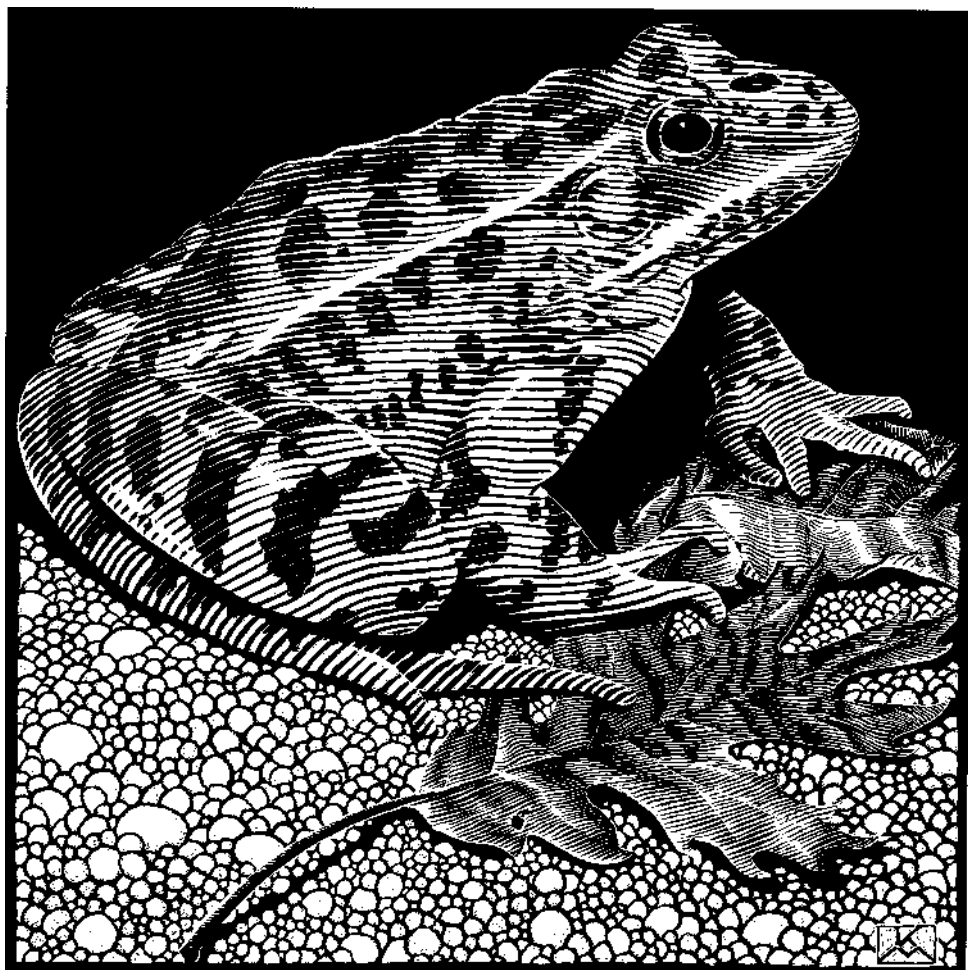


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INTRODUCTION

The plains leopard frog, *Rana blairi* (fig. 1), has its distribution centered in the Great Plains (Black 1976; Brooks 1976; Brown 1992; Collins 1982; Dixon 1987; Dunlap and Kruse 1976; Hammerson 1982; Hillis 1981; Lardie 1982; Littlejohn and Oldham 1968; Lynch 1978, 1985; Mecham et al. 1973; Pace 1974; Post and Pettus 1966). However, an aggregate of populations is isolated in southeastern Arizona (Clarkson and Rorabaugh 1989; Frost and Bagnara 1977; Frost and Platz 1983), and an eastern extension of the range occurs in the Prairie Peninsula of the Midwest (Axtell 1977; Brown 1992; Brown and Brown 1972; Christiansen and Bailey 1991; Johnson 1987; Pace 1974). In the Prairie Penninsula extension, *R. blairi* occurs primarily in southern Iowa (Christiansen and Bailey 1991), the northern half of Missouri (Johnson 1987), and in a wide band across the central part of Illinois (Axtell 1977; Brown 1992; Brown and Brown 1972; Pace 1974). The purposes of our paper are to (1) report distributional information for *R. blairi* along the Mississippi River south of the main range of the species in the Prairie Peninsula, (2) summarize information on habitats in this area as well as in the Great Plains and Prairie Peninsula, and (3) discuss the zoogeography of the species.

DISTRIBUTION

In 1974 Pace reported a locality for *R. blairi* near the Mississippi River in extreme southern Illinois (Alexander Co.: Horseshoe Lake Dam, UMMZ 84301; see appendix for listing of acronyms and catalog numbers) a considerable distance from the more northern localities then known for the species. This record is unusual because (1) the Horseshoe Lake locality is far south of the Prairie Peninsula and (2) the habitat at Horseshoe Lake (Smith 1961) is typical of the Austroriparian Biotic Province characteristic of the southeastern United States (Dice 1943). This habitat is rare in Illinois and vastly different from the prairie further north in central Illinois and Missouri. We reexamined UMMZ 84301, however, and the specimen is definitely *R. blairi*.¹

Fig. 1. Plains leopard frog (*Rana blairi*). (Photograph by T. R. Johnson.)



During an examination of preserved leopard frogs from museums and collections in Illinois, we uncovered four additional specimens of *R. blairi* from the Horseshoe Lake area (UIMNH 26756, 26758; FMNH 23465, 23466), and subsequent fieldwork confirmed a small extant population. During the course of additional fieldwork and further examination of preserved specimens, we found another 12 locality records for *R. blairi* in southeastern Missouri and southern Illinois (fig. 2; appendix). Axtell (1977) provided two additional records of adults in Perry County, Missouri, and St. Clair County, Illinois; Trauth et al. (1992) reported one adult from Mississippi County, Arkansas. The majority of the locality records ($n=12$, 80%; the records around Horseshoe Lake are treated as one locality, as are those near Gorham, Illinois) are from the floodplain of the Mississippi River. Three (20%) were recorded only a short distance away from the floodplain. Thus the range of *R. blairi* clearly has an elongated extension along the Mississippi River southward from the main distribution in the Prairie Peninsula.

HABITAT

Prior to European settlement, much of the habitat of *R. blairi* in the Prairie Peninsula and Great Plains probably was prairie and adjacent habitats (Brown 1992). However, since most prairies in Illinois, Missouri, and elsewhere have been destroyed by agriculture, *R. blairi* is now encountered in a variety of habitats. In light of the probable past association of *R. blairi* with prairie in the Great Plains and Prairie Peninsula, we review the evidence for prairie along the portion of the Mississippi River under consideration (fig. 2).

The present habitat in this area undoubtedly differs vastly from the habitat that existed before European settlement. Probably the most significant environmental modifications were the construction of (1) levees along the Mississippi River and its major tributaries to constrain prolonged inundation and (2) ditches to drain the wetlands. These alterations allowed extensive development of agriculture on the rich alluvial bottomlands although substantial stands of forest are still present.

Referring to the "prehistoric period," Gleason (1922:78) wrote that "the wide alluvial bottom lands of the larger rivers, notably the Missouri, Mississippi, and Illinois, seem to have resisted forest invasion, and on them the forests were limited to relatively narrow strips along the channel and the abandoned oxbows, alternating with strips of prairie." He noted that numerous early observers reported this, though he did not indicate specific geographical regions.

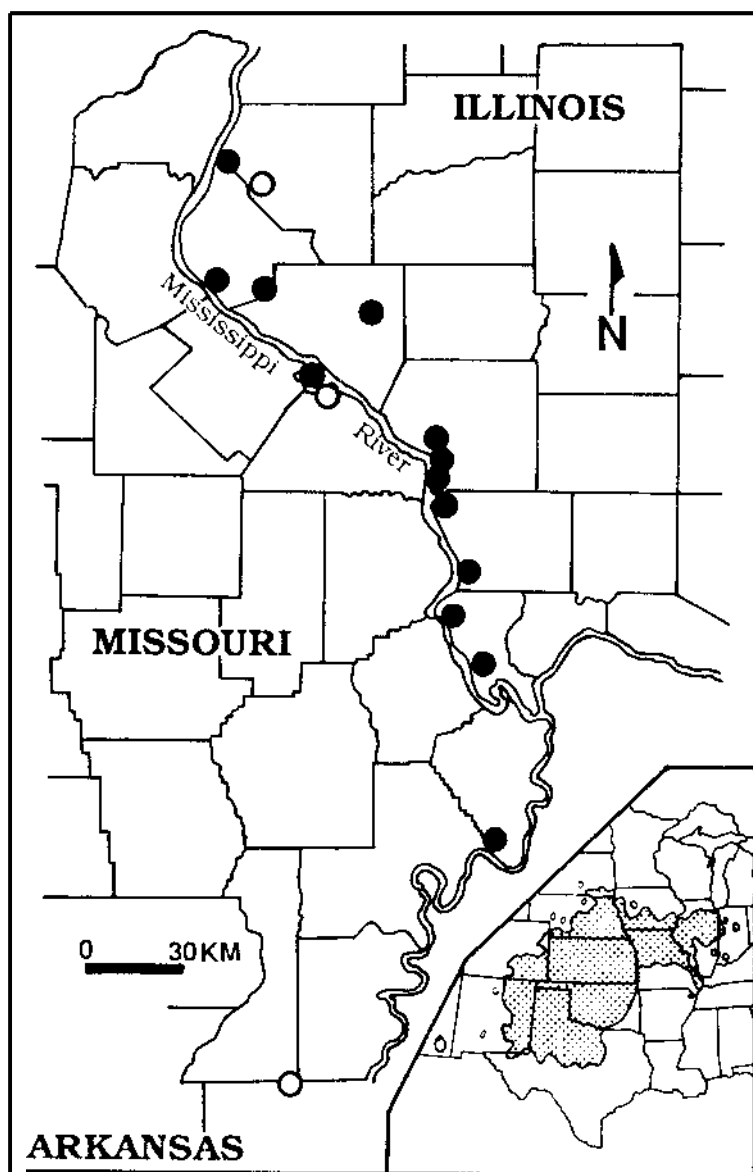
In a more detailed study, Anderson (1970) examined original land survey records completed before 1820 and mapped the presettlement distribution of prairies in Illinois. His map shows absence of prairies and predominance of other vegetation types such as forest and savannah (R. C. Anderson, pers. com.) along the Mississippi River from St. Clair through Alexander counties. However, R. C. Anderson (pers. com.) recently found a stand of prairie along the railroad track near Illinois State Highway 3 on the floodplain of the Mississippi River in Union County, Illinois. This prairie may have had a presettlement origin, or humans may have brought in propagules of prairie plants during or after the building of the railroad.

Evers (1955) described a number of hill prairies along the Mississippi River from St. Clair through Alexander counties, Illinois. These small prairies occur in extremely xeric environments (for the Midwest) on the upper slopes (often steep) and brows of bluffs (Evers 1955), and consequently, they are probably poor habitats for leopard frogs.

Prairies were somewhat more evident along the floodplain of the Mississippi River in southeastern Missouri. Schroeder (1983) examined original land survey records (in a manner similar to Anderson [1970] for Illinois) and mapped presettlement distribution of prairies and nonprairies in Missouri. He found that the southeastern lowlands were heavily timbered, but isolated prairies did occur on the floodplain of the Mississippi River in St. Genevieve, Perry, Scott, Mississippi (also see Transeau [1935]), and Stoddard counties.

King and Allen (1977) examined fossil pollen from 9000-3000 yr BP (radiocarbon dated years before present) in a sediment core taken from an old channel of the Mississippi River

Fig. 2. Distributional records for the plains leopard frog (*Rana blairi*) along the Mississippi River in southern Illinois, southeastern Missouri, and northeastern Arkansas. • = localities of specimens we examined (the records around Horseshoe Lake, Alexander County, Illinois, are plotted as one locality). ○ = literature records. Inset shows the entire range of *R. blairi*.



near Advance, Stoddard County, Missouri (ca. 41.5 km west of Horseshoe Lake, Illinois). Pollen from before 8700 yr BP and after 5000 yr BP was predominantly arboreal, indicative of bottomland forest. However, from 8700-5000 yr BP nonarboreal pollen (grasses, herbs) became dominant. The high percentages of Gramineae (up to 70%) reported by King and Allen (1977) are even greater than those formerly reported for modern grassland communities in North America. Consequently, King and Allen (1977) concluded that the period 8700-5000 yr BP represented the time of maximum expansion of the Prairie Peninsula into southeastern Missouri. Moreover, prairie was also present in northeastern Arkansas (Anderson 1983; Arkansas Dept. of Planning 1974).

Thus, during the middle Holocene along the Mississippi River in southern Illinois, southeastern Missouri, and northeastern Arkansas, sufficient prairie was probably present to allow colonization by *R. blairi*, though prairie vegetation probably did not predominate as it did in the Prairie Peninsula to the north.

ZOOGEOGRAPHY

Blair (1958, 1965) was a foremost proponent of a formerly influential Pleistocene zoogeographic theory (previously proposed in abbreviated form by Adams [1902] and Deevey [1949]), which suggested that southward glacial movements and accompanying cold climates in front of the glacial rim during the Pleistocene resulted in the fragmentation of the ranges of many warm-adapted species as they withdrew into refugia in Mexico and Florida. Supporting evidence was drawn primarily from analyses of pollen profiles, existing animal distributions, and then-available Pleistocene fossils (mainly plants and tetrapod vertebrates).

An alternate Pleistocene zoogeographic theory, the equable climate model, was originally defined by Hibbard (1960) and Hibbard and Taylor (1960). Graham and Mead (1987:372) have succinctly articulated this theory as follows: "During glacial stages, species were physically forced southward by glacial ice in North America. However, resident species south of the ice sheet were not displaced en masse, because winter extremes were not accentuated. Boreal and arctic taxa were integrated with preexisting temperate communities under the more equable climatic conditions." Evidence for this model from the Pleistocene mammalian fauna is particularly convincing, but further substantiation is also provided by other Pleistocene vertebrate and terrestrial invertebrate faunas as well as vegetation (Graham 1985). Reptilian and amphibian evidence has been summarized by Holman (1980). Several other studies have indicated that there was little geographic movement of reptile and amphibian species during the Pleistocene in North American midlatitudes (Holman 1992). Furthermore, Van Devender and Mead (1978) found no indication of the restriction of desert herpetofaunas to refuges in Mexico during late Pleistocene glaciation.

It is clear that during the Wisconsinan it was impossible for *R. blairi* to occupy the extensive area covered by glaciation in Illinois. However, the extent to which the edge of the range of *R. blairi* shrank southward from its pre-Wisconsinan northern boundary in the Great Plains is conjectural. The present distribution of the species extends as far northward as southern South Dakota (Dunlap and Kruse 1976), and presumably the species has considerable cold tolerance. Furthermore, Holman (1992) reported Wisconsinan fossils of the "*Rana pipiens* group" (could be *R. pipiens*, *R. blairi*, or *R. sphenoccephala* [see endnote 2]) at three sites in Michigan and Indiana from 15-12 ka BP. These sites are not all that far from the margin of the ice rim that existed at those times (Holman 1992). Some landforms imply prior existence of permafrost near the ice front, and fossil tundra plants and animals also indicate discontinuous tundra-like conditions (Pielou 1991). However, this zone was relatively narrow (Wright 1987). Further south there was a band of boreal forest, but this band also was narrow (Wright 1987) and probably distributed in a mosaic with grassland (Rhodes 1984; Wright 1987).

Pollen sequences have indicated spruce forest as far south as northeastern Kansas (Muscotah and Arrington), the Ozark Highlands of Missouri (Boney Spring and other sites), and southern Illinois (Seminary School basin), but these sites have been interpreted to be wetlands covered with spruce (Wright 1987). It is possible that in the northern part of its range during the glacial maxima, *R. blairi* may have occupied forest or a mosaic of forest and grassland (which may have been less than optimal habitat). After the Wisconsinan glaciation, it was possible for *R. blairi* to expand its range northward in the Great Plains (if indeed, the northern edge of the species range did shrink in that area during the Wisconsinan). In the early to middle Holocene, a warm, arid climate prevailed (Pielou 1991). Smith (1957) suggested that a number of prairie-adapted species from the Great Plains dispersed into the Prairie Peninsula during this warm, arid period, and Pace (1974) further suggested that *R. blairi* may have extended its range eastward during or after the expansion of the Prairie Peninsula. However, many amphibians are quite sensitive to aridity because they are easily desiccated. Consequently, the warm, arid period during the Holocene may not have been the most favorable time for major amphibian migrations.

An optimal time for *R. blairi* to have moved eastward during the Holocene may have been after the warm, arid period and after the establishment of prairie. However, the warm, arid climate did not occur in all areas concurrently. For example, pollen analysis from northeastern Iowa (Chumbley et al. 1990) indicated that the warm, arid period and establishment of prairie occurred at that location in the late Holocene. Thus, *R. blairi* could have dispersed into the Prairie Peninsula during a moist period in the early Holocene, particularly if the species could have occupied forest habitats or a mosaic of forest and grassland. R. W. Graham (pers. corn.) has suggested that this dispersal might have occurred even in the late Pleistocene. Paleontological investigations by Holman (1992) indicated that numerous herpetological species (including leopard frogs) had reinvaded, from the south, several sites in Indiana, Michigan, and Ohio by 15-14 ka BP, 13-12 ka BP, 11-10 ka BP, 6-4 ka BP, and 4-3 ka BP. Prevailing climates

and type of habitat present in different geographical regions undoubtedly dictated the time(s) and rate(s) at which *R. blairi* became established in the Prairie Peninsula since the late Pleistocene.

It seems unlikely that *R. blairi* colonized the area along the Mississippi River in southern Illinois, southeastern Missouri, and northeastern Arkansas by direct eastward migration over the Ozark Plateau in the southern half of Missouri and northern Arkansas because of the more elevated, uneven terrain, and because Schroeder's (1983) maps show that presettlement prairies were small, isolated, and uncommon in southern Missouri (except in the west). A more plausible migration route could have been southward from the Prairie Peninsula in Illinois, as Anderson's (1970) map shows the extension of discontinuous presettlement prairie into the eastern portions of St. Clair, Monroe, and Randolph counties, Illinois. The species may also have dispersed down the valley of the Mississippi River, which may thus have served as a surrogate prairie, as the floodplain of the Mississippi River and the Grand Prairie share certain topographic, edaphic, climatic, and vegetational similarities.

Axtell and Haskell's (1977) study of the chorus frog, *Pseudacris streckeri*, suggests an alternate (although less likely) dispersal route for *R. blairi*. The main body of the distribution of *P. streckeri* is in Texas and Oklahoma (Smith 1966), but isolated populations (summarized by Brown and Rose 1988) occur along the Illinois River in west-central Illinois, along the Mississippi River in southwestern Illinois, in extreme southern Illinois, in southeastern Missouri and northeastern Arkansas, and at several locations in northwestern Louisiana and west-central Arkansas, the most significant being along the Arkansas River. Axtell and Haskell (1977) suggested that the most probable Holocene dispersal route for *P. streckeri* from the southwestern United States was across Arkansas on the Arkansas River floodway, and up the Mississippi River floodplain to Illinois. Some prairies have been found along the Arkansas River and in northeastern Arkansas (Anderson 1983; Arkansas Dept. of Planning 1974), and thus, *R. blairi* may have followed a dispersal route similar to that proposed for *P. streckeri*. However, the only locality record known for *R. blairi* in Arkansas (Trauth et al. 1992) is in the extreme northeast, although the distribution of leopard frogs in that state has not been studied extensively. Also, the known locality records for *R. blairi* in Texas and Oklahoma are a considerable distance from the presumptive dispersal route along the Arkansas River in Arkansas.

Another explanation for the origin of *R. blairi* in southern Illinois, southeastern Missouri, and northeastern Arkansas involves the dispersal of the species into the area at some time prior to the Wisconsinan, either from the north or the south. During the Wisconsinan, isolated populations of *R. blairi* may have survived in favorable refugia south of the glaciers in southern Illinois, southeastern Missouri, and northeastern Arkansas (or perhaps even further southward). Intervening populations between that area and the Great Plains could have been extirpated by climatological and/or geological changes. After the Wisconsinan, the species could then have moved northward along the Mississippi River, eventually meeting the populations in the Prairie Peninsula. At present, the small population sizes and spotty distribution of *R. blairi* along the Mississippi River in southern Illinois and southeastern Missouri make it difficult to envision

the area as a major refugium. However, if *R. blairi* was successfully able to inhabit forests during the Pleistocene, a refugium in that area (or further southward) is plausible.

We feel that the most likely origin for *R. blairi* along the Mississippi River in southern Illinois, southeastern Missouri, and northeastern Arkansas was by southward dispersal from the Prairie Peninsula during the Holocene or perhaps the late Pleistocene, though the other two scenarios have their merits if certain conditions were prevalent during the Pleistocene and Holocene.

SUMMARY

The present distribution of the plains leopard frog (*Rana blairi*) is primarily in the Great Plains and Prairie Peninsula. Before European settlement, the habitat was probably in prairie and adjacent areas. *Rana blairi* most likely dispersed into the Prairie Peninsula from the Great Plains sometime during the Holocene or perhaps the late Pleistocene. Discovery of localities along the Mississippi River in southern Illinois, southeastern Missouri, and northeastern Arkansas indicates an extension of the range of the species south of the Prairie Peninsula. The ability of *R. blairi* to occupy habitats peripheral to prairies, and the presence of scattered Holocene prairies, apparently allowed the species to disperse along the Mississippi River, most likely by an unusual southward migration from the Prairie Peninsula during the Holocene or perhaps the late Pleistocene. Two other dispersal alternates, both from the south, are possible if certain conditions were present during the Pleistocene and Holocene.

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ENDNOTES

1. Two specimens from Horseshoe Lake Dam were cataloged under museum number UMMZ 84301: one is *R. blairi* and the other is *Rana sphenoccephala*.
2. Holman (1972) indicated that leopard frogs (*Rana pipiens sensu lato*) have been the most consistently reported anuran fossils from the Pleistocene of the U.S. Furthermore, many Pleistocene leopard frog fossils have been found within the present range of *R. blairi* but allopatric to other species of leopard frogs (summarized by Brown 1992). These specimens have been assigned to *R. pipiens, sensu lato*, *R. pipiens* complex, or *Rana* sp. indet. Rogers (1984) could not, however, separate the bones of *R. blairi*, *R. sphenoccephala*, and *R. pipiens, sensu stricto*. Likewise, Holman (1977) found no consistent differences in the ilia of these three species and *R. berlandieri*. Thus, it is probably not possible at present to distinguish fossils of different sibling species of leopard frogs (Brown 1992). Consequently, the fossil record of *R. blairi* is currently of no help in unraveling the zoogeographic past of the species.

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APPENDIX: LOCALITY DATA FOR DISTRIBUTIONAL RECORDS OF RANA BLAIRI.

Catalog numbers are given for preserved museum specimens. An asterisk (*) indicates that the specimen(s) were caught, examined, and released in the field, or were found dead on the road. Acronyms for museums/collections appear at the end of the appendix.

Illinois. *Alexander County*: 0.5 km SSW Gale, 1 specimen;* Horseshoe Lake, FMNH 23465, 23466; Horseshoe Lake Island, UIMNH 26756, 26758; near Horseshoe Lake Motel, just SW of Illinois State Highway 3, SE Olive Branch, 3 specimens;* along Miller City-Olive Branch Road, 5 specimens.* *Jackson County*: Gorham fish farms, MAM 498; 3.6 km S Gorham, 1 specimen;* Grand Tower, across from Hale's restaurant, small chorus;* NW of junction of Illinois State Highway 3 and the Big Muddy River, small chorus.* *Monroe County*: 1.1 mi (1.8 km) S and 1.7 mi (2.7 km) W Ames, 38° 07' 48" N, 90° 05' 04" W, SIUE 2682; near junction of Buff and Ivy roads, near Fults, 38° 10' 01" N, 90° 13' 22" W, SIUE 2681. *Randolph County*: Kaskaskia Island, SIUC 3782-3785; 4 mi (6.4 km) S Sparta, SIUC 3184. *St. Clair County*: 2 mi (3.2 km) S Dupu along Illinois State Highway 3, 38° 29' 20" N, 90° 13' W, SIUE 2680. *Union County*: Union County Conservation Area, ISM 622335; "In woods," SIUC 113, 2 specimens (not plotted in fig. 2).

Missouri. *Mississippi County*: Big Oak Tree State Park (Ten Mile Pond area), SE East Prairie, MDC uncatalogued, 4 specimens (others observed).*

Acronyms for museums/collections: FMNH, Field Museum of Natural History; ISM, Illinois State Museum; MAM, Michael A. Morris Collection; MDC, Missouri Dept. of Conservation; SIUC, Southern Illinois University at Carbondale; SIUE, Southern Illinois University at Edwardsville; UIMNH, University of Illinois at Urbana-Champaign Museum of Natural History; UMMZ, University of Michigan Museum of Zoology.

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